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Diversity and systematics of Haminoeidae gastropods (Heterobranchia: Cephalaspidea) in the tropical West Pacific Ocean: new data on the genera *Aliculastrum*, *Atys*, *Diniatys* and *Liloea*

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Abstract

Four genera of Haminoeidae gastropods inhabiting the tropical West Pacific (*Aliculastrum*, *Atys*, *Diniatys*, and *Liloea*) were studied based on the combined analyses of live animals, external morphology, anatomy and shells aided by scanning electron microscopy and molecular sequencing. Eleven species are described including two new to Science, namely *Atys pittmani* sp. nov. and *Atys ukulele* sp. nov.. The putative synapomorphies of the genera *Aliculastrum*, *Diniatys*, and *Liloea* are discussed. High levels of morpho-anatomical variability were found among representatives of the genus *Atys*, which hampered the recognition of synapomorphies.

Key words: Mollusca, cephalaspids, bubble-shells, diversity, taxonomy

Introduction

Haminoeidae is the most genera-rich family of Cephalaspidea gastropods (Burn & Thompson 1998). It was first proposed by Pilsbry (1895) with the name Hamineinae as a subfamily of Akeridae with the single genus *Haminea* (= *Haminoea*). Species in this family are found worldwide in both tropical and temperate waters. Their shells show great variability ranging from typical bulloid to cylindrical-elongate. Spiral grooves can be present either at the ends or covering the entire shell. Shells are usually thin, translucent, and fragile but some species in the genera *Atys* and *Aliculastrum* possess solid thick shells. The mantle and other body parts are usually dull and cryptically coloured, although some species can be colourful and be even capable of changing colour to suit the environment (Edlinger 1982; Gosliner *et al.* 2008). They have a muscular buccal bulb containing chitinous jaws and a radula formed by a central tooth that varies in shape between genera plus hook-shaped lateral teeth in variable numbers. A gizzard is present with three plates containing pointed rods for shredding algal tissue and diatoms, the main diet of haminoeids (Gosliner 1991; Mikkelsen 1996; Malaquias *et al.* 2009a; Malaquias 2010).

Thirteen to 17 genera are often recognized as valid in recent literature, namely *Aliculastrum* Pilsbry, 1896, *Atys* Montfort, 1810, *Austrocylichna* Burn, 1974, *Bullacta* Bergh, 1901, *Cylichnatys* Kuroda & Habe, 1952, *Cylichnium* Dall, 1908, *Diniatys* Iredale, 1936, *Haloea* Pilsbry, 1921, *Hamineobulla* Habe, 1950, *Haminoea* Turton & Kingston, 1930, *Liloea* Pilsbry, 1921, *Limulatys* Iredale, 1936, *Mnestia* H. Adams & A. Adams, 1854, *Nipponatys* Habe, 1952, *Phanerophthalmus* Adams, 1850, *Smaragdinella* Adams & Reeve, 1848, and *Weinkauffia* Monterosato, 1884 (Habe 1952; Burn & Thompson 1998; Carlson & Hoff 2003; Qi 2004; Gosliner *et al.* 2008; Bouchet 2014). Malaquias *et al.* (2009b) showed by molecular phylogenetic analysis that contrary to the traditional view, *Ventomnestia* is not part of Haminoeidae and later (Malaquias, 2010) confirmed the inclusion of the genera *Atys*, *Bullacta*, *Haminoea*, *Phanerophthalmus*, and *Smaragdinella* in the family using multi-locus Bayesian molecular phylogenetics.

Several studies have been conducted in the West Pacific since the 19th century and major expeditions yielded significant contributions to the knowledge of cephalaspids in the region. The Astrolabe Expedition produced some

do not possess ovoid inflated robust shells as the type species *A. naucum*, but instead elongated and fragile shells. Unfortunately, specimens of the type species *A. naucum* were not available for anatomical dissection but this species has been extensively studied before (e.g. Bergh 1901; Lin 1997; Carlson & Hoff 1999). According to Bergh (1901), *A. naucum* possesses a radula with 70 rows of teeth with a triangular median tooth. While documenting similar median tooth character, Lin (1997) referred to the presence of smaller triangular cusps at both sides of the median tooth. Both Bergh (1901) and Carlson & Hoff (1999) referred that gizzard plates have a high number of fine ridges, and the latter authors mentioned the presence of tiny rods on top of ridges.

Clarification of the generic status of species traditionally included in the genus *Atys* would require a broader study encompassing species from all biogeographic regions. However, preliminary molecular phylogenetic data (Too 2011) rendered traditional *Atys* paraphyletic. Until a sound phylogenetic framework is available for the relationships of haminoeidae gastropods we suggest using *Atys* in its traditional sense (*sensu* Burn & Thompson 1998).

Diniatys—Species of this genus have a strongly calcified callus at the end of columella folding outwardly that can resemble a tooth-like projection. This seems to be a synapomorphy of the genus. Anatomically, species of *Diniatys* have a male reproductive system with a fine and long seminal duct that is at least twice as long as the elongated penial region. This is unique among haminoeidae gastropods and can also be considered a synapomorphic trait of the genus.

Liloa—Recognized synapomorphies of the genus are the presence of spiral grooves covering the translucent shells more or less regularly spaced throughout; gizzard plates lacking rachis with ridges organized parallel to each other with pointed rods densely arranged on both anterior and posterior sides and a single row of larger pointed rods along the top margin; presence of two seminal ducts in the male reproductive system, one of them having a hook-like posterior end.

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